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PHENOLOGY, REPRODUCTIVE CYCLES, AND SPECIES COMPOSITION OF A DUNG BEETLE COMMUNITY (COLEOPTERA: SCARABAEOIDEA) FROM A HIGH MOUNTAIN PASTURE SYSTEM ON THE ORIENTAL NEOVOLCANIC AXIS (VERACRUZ, MEXICO)

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Abstract.—This 13-month study focused on a dung beetle community in the high mountain pastures of the Oriental Neovolcanic Axis, near Tonalaco, a site located on the southeastern slope of the Cofre de Perote volcano (Veracruz, Mexico), at an altitude of 2620 meters. A total of 1997 individuals from seven dung beetle species were collected in monthly samples of cattle and horse dung. These species included one Geotrupinae, *Geotrupes (Halffterius) rufoclavatus*; five Aphodiinae species, *Blackburneus (sensu lato) charmionus, Chilothorax ornatus, Gonaphodiellus opisthius, Oxyomus setosopunctatus*, and *Planolinellus vittatus*; and, one Scarabaeinae, *Onthophagus chevrolati*. Phenology and reproductive cycles were analyzed for the three most abundant species. *Gonaphodiellus opisthius* showed two population peaks significantly associated with the rainy season and the precipitation, and they were strongly univoltine. In contrast, *P. vittatus* and *O. chevrolati* seemed associated with the dry season, although they were also collected in the rainy season. They were multivoltine. Species composition was also analyzed for other dung beetle similar studies on the Oriental Neovolcanic Axis. In general, eight dung beetle species showed especially characteristic from these localities (the last five former species plus *Cephalocyclus durangoensis, C. hogei*, and *Liothorax levatus*). Most of the dung beetles from the Oriental Neovolcanic Axis present univoltine reproductive cycles, as a consequence of their high mountain adaptation. Moreover, they are principally distributed at the Mexican Transition Zone and Mesoamerica, and could be considered as Nearctic elements.

Resumen.—El presente estudio, desarrollado durante 13 meses, tuvo como objetivo estudiar la comunidad de los escarabajos del estiércol de pastos de alta montaña de la región oriental del Eje Neovolcánico, cerca de Tonalaco, localidad situada en la ladera sudeste del volcán Cofre de Perote (Veracruz, México). Se colectó un total de 1997 individuos, pertenecientes a siete especies de escarabajos del estiércol, mediante muestreos mensuales realizados en excremento de vaca y caballo. Estas especies incluyeron un Geotrupinae, *Geotrupes (Halffterius) rufoclavatus*; cinco Aphodiinae, *Blackburneus (sensu lato) charmionus, Chilothorax ornatus, Gonaphodiellus opisthius, Oxyomus setosopunctatus* y *Planolinellus vittatus*; y, un Scarabaeidae, *Onthophagus chevrolati*. Se estudiaron la fenología y los ciclos reproductivos para las tres especies más abundantes. *G. opisthius* mostró dos picos poblacionales significativamente asociados con la estación de lluvias y con las precipitaciones, y se comportó marcadamente univoltino. Por el contrario, *P. vittatus* y *O. chevrolati* se mostraron posiblemente asociados con la estación seca, aunque también se colectaron durante la estación de lluvias; se comportaron como multivoltinos. Se analizó también la composición de especies para otros estudios de escarabajos del estiércol realizados en la región oriental del Eje Neovolcánico. En general, ocho especies de escarabajos del estiércol son especialmente características de estas localidades (las cinco primeras especies anteriormente nombradas más *Cephalocyclus durangoensis, C. hogei*, and *Liothorax levatus*). La mayoría de los escarabajos estercoleros de la región oriental del Eje Neovolcánico tienen ciclos univoltinos, como consecuencia de su adaptación a alta montaña. Además, presentan principalmente una distribución comprendida en la Zona de Transición Mexicana y Mesoamérica, y se podrían considerar como elementos Neárticos.

Key Words: dung beetles, Aphodiinae, Scarabaeinae, Geotrupinae, Oriental Neovolcanic Axis, phenology, reproductive cycles, geographic distribution

High mountain habitats are a very interesting setting for ecological studies because of the seasonal and predictable changes in environmental conditions. Communities of dung beetles usually inhabit high mountain pastures worldwide (Lumaret and Stiernet 1991), and therefore they also populate tropical and subtropical regions of the Northern Hemisphere (Kohlman 1991). These dung beetle communities are generally dominated by Aphodiinae (Coleoptera: Scarabaeoidea: Scarabaeidae) (Hanski 1991), although it is possible to find species belonging to other groups, such as Geotrupidae (Coleoptera: Scarabaeoidea) and Scarabaeinae (Coleoptera: Scarabaeoidea: Scarabaeidae). Most of these species are coprophagous feeders, although some are euriphagic and saprophagous species that could alternately or occasionally share the habitat and the food (Halffter and Edmonds 1982).

Dung beetles are ecologically important in pasturelands because of their recycling of nutrients (Fincher 1981, Rougon et al. 1988, Yokohama et al. 1991) and control of livestock parasites (Bryan 1973, Fincher 1975, McQueen 1975, McQueen and Beirne 1975, Chirico et al. 2003) and flies (Moon et al. 1980, Ridsdill-Smith et al. 1987, Ridsdill-Smith and Hayles 1990). However, dung beetles are possibly one of the most sensitive and often-damaged groups of high mountain pasture systems, as a consequence of changes in land use and chemical applications (vermicides and herbicides) (Lumaret and Martínez 2005, Martínez and Lumaret 2006). Therefore, the study of the biology and peculiarities of dung beetle communities is necessary to understand the natural processes of these systems and then to try to minimize possible impacts which could bring significant effects on the environment balance.

The Neovolcanic Axis is a mountain system situated in Central Mexico, between the 17°15′–21°14′N and 96°9′–105°16′W coordinates. It extends from northwest to southeast more than 1,000 km long and 50–150 km wide. The Neovolcanic Axis started to form during the Oligocene, although it underwent more intense development during Pliocene-Pleistocene (Halffter 1987). In this study, a community of dung beetles from a high mountain pasture (>2500 meters above sea level), situated on the southeastern slope of the Cofre de Perote volcano, at the Oriental Neovolcanic Axis, was observed and analyzed throughout a year.

Several other studies have already analyzed the phenology and reproductive biology of some Mexican dung beetles, especially Aphodiinae (Halffter et al. 1985; Martínez 1992, 2001, 2003, 2005; Martínez et al. 1996, 1998, 2000, 2001a, 2001b; Cruz and Huerta 1998; Martínez and Cruz 1999, 2002; Martínez and Alvarado 2001; Cruz et al. 2002; Martínez and Suárez 2006). This study examines the abundance of the different species, the species' reproductive cycles, and local climatic data to determine possible relationships and to describe the community.

Additionally, to determine the importance of the dung beetle communities situated on high mountain pastures of this region, other previous similar studies conducted at the Oriental Neovolcanic Axis have been also considered (Cruz et al. 2002, Martínez 2005, Martínez and Suárez 2006). Thus, reproductive cycles and geographic distribution of cited species have been analyzed jointly to explain the composition and importance of these communities and to characterize them.

MATERIALS AND METHODS

Study area.—The sampling was carried out in a grassland area where some horses and cattle usually graze, on the southeastern slope of the Cofre de Perote volcano (19°25′59″N, 97°7′51″W, 2620 meters), close to Tonalaco village, Xico municipality, Veracruz State, Mexico (Fig. 1). The sampling area was situated in a rainforest area, with induced pastures and pine-oak forests (Rzedowski 1978). The weather is temperate, with an annual mean temperature of 12.3°C, which ranges between 2.5 and 21.9°C of minimum and maximum temperatures respectively, and with a total annual precipitation of 908 mm (data generated through interpolation of average monthly climate data from world weather stations, covering a 30- to 50-year period; database from Hijmans et al. 2006; Fig. 2). Data from the closest climatic station Oxtlapa (around 5 km away; National Water Commission, State of Veracruz) was not taken into account as it was situated at an elevation of 1850 meters.

Collecting methods.—The insects were collected monthly, from February 2005 through February 2006. Ten dung pat samplings of about 250 grams each were taken once a month. These samplings were selected from cattle and horse dung with an external crust and an internal semi-moist consistency. Along with the dung, two centimetres of soil underneath were also examined for each sampling. Temperature and humidity measures and general climatic conditions at the moment of sampling were also noted down. All the dung beetles from these samplings were manually gathered, identified, and counted at the laboratory.

Species phenology.—Individuals of each species and species richness were counted from February 2005 through February 2006. Correlations between species richness and number of individuals per month were analyzed in the context of climatic variables. Climatic data taken at time of sampling as well as the world climatic database of Hijmans et al. (2006) were used to check correlations, the latter extracting monthly data (mean, minimum, and maximum temperatures and total precipitation) for the Tonalaco location according to its geographic coordinates (≈1 km error). Correlations were rectified by means of the Bonferroni correction.

Moreover, monthly data were also separated according to yearly seasons, dry (from November to the beginning of May) and rainy (from the end of May to October), and the groups were statisti-

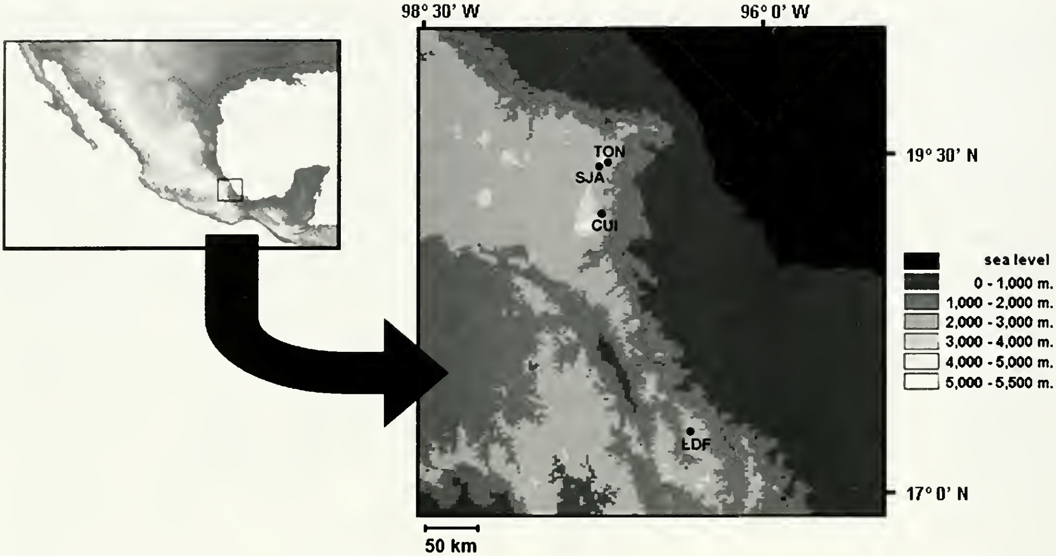

Fig. 1. Geographic location of the Tonalaco locality (Veracruz, México). The location of three other annual dung beetles studies are also shown on the map (CUI: Cuiyachapa; LDF: Llano de las Flores; SJA: San José Aguazuelas; TON: Tonalaco).

cally compared for species richness and number of individuals.

Reproductive cycles.—To determine the reproductive cycles of the species, the study considered dung beetles gathered from March 2005 through February 2006. Species were selected for examination of their reproductive cycles depending on whether a considerable number of specimens had been collected for the species and whether they appeared during several months over the sampling period. Whenever possible, at least 10 individuals of each species were chosen at random and their reproductive systems were dissected in Ringer-Ephrussi saline solution. The reproductive systems were fixed in AFTAD (96% ethanol – formaldehyde – trichloroacetic acid – dimethylsulfoxide) and subsequently preserved in 96° ethanol. Most of these samples were also dyed in toto with Feulgen-green light (Martínez 2002).

For female gonads, three maturing stages were discriminated: immature, mature/maturing before oviposition, and mature after oviposition. For males, three stages were also considered: immature, mature/maturing before copulation, and mature after copulation. Ovarian activity was determined for each female according to the length of basal oocytes, the appearance of chorion, and the wideness and laxity of the lateral oviducts. Male testicular and glandular activity was determined taking into account the length of testis follicles, volume of the accessory gland reservoirs, and presence of seminal fluid in the gland ducts and reservoirs (Martínez 2002).

This method was chosen because it has been satisfactorily carried out with other Scarabaeidae species (Martínez 1992a, 1992b, 2005; Martínez and Cruz 1992, 2002; Martínez et al. 1996, 1998; Cruz and Huerta 1998; Cruz et al. 2002).

Completeness of inventories and characterization of dung beetle communities.– Reliability of the species inventory obtained in the samples was evaluated by using non-parametric estimators of species richness, Chao2 and ACE (Chao 1987, Colwell and Coddington 1994,

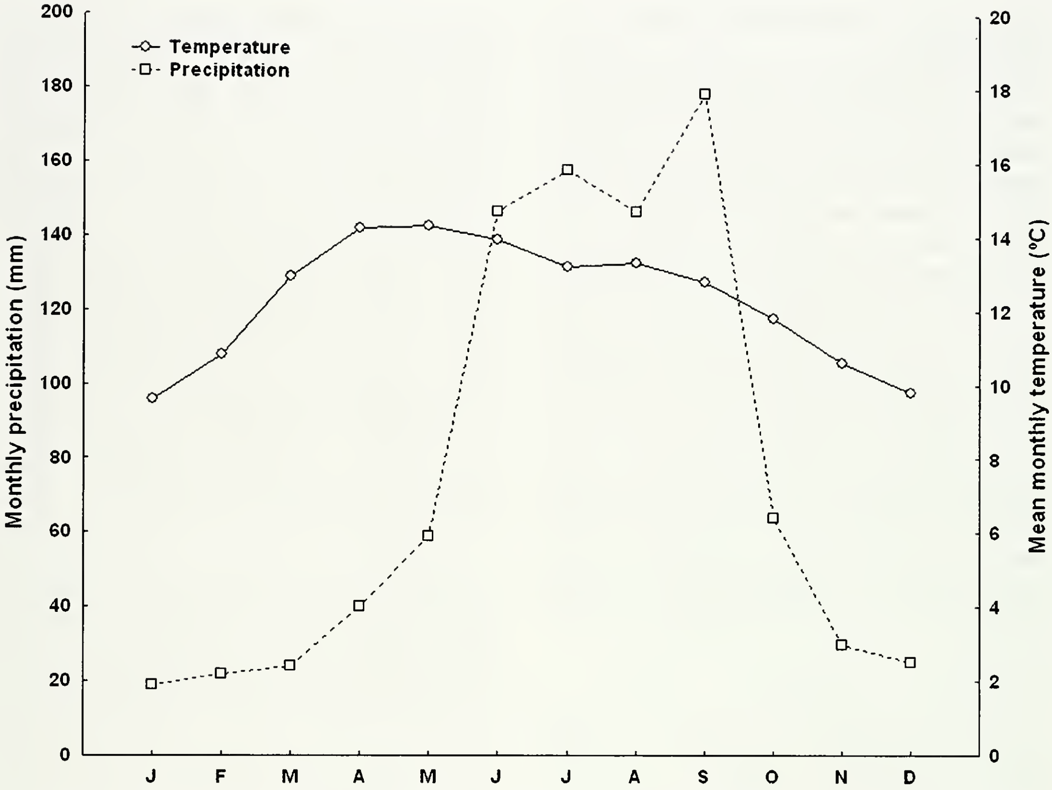

Fig. 2. Ombrothermic chart for Tonalaco (Veracruz, Mexico) station (19°25′59″N, 97°7′51″W, 2620 meters; Hijmans et al. 2006). Note that the precipitation axis is 10 times the temperature axis, instead of two times, as is usual for ombrothermic charts.

Chazdon et al. 1998). The values of estimators were obtained by means of the EstimateS program (Colwell 2005).

Three other annual dung beetle studies carried out in localities on high mountain pastures (>2500 m) in the Oriental Neovolcanic Axis (Fig. 1) were also analyzed this way in order to confirm if their sampling efforts had been suitable: (CUI) Cuiyachapa, at an altitude of 2700 m, on the eastern side of the Pico de Orizaba volcano, Veracruz (Cruz et al. 2002); (SJA) San José de Aguazuelas, at 2700 m, on the southwestern slope of the Cofre de Perote volcano, Veracruz (Martínez 2005); and (LDF) Llano de las Flores, at an altitude of 2600 m, on the eastern slope of the Sierra de Juárez, Oaxaca (Martínez and Suárez 2006). The original record sheets of these three studies were accessed and consulted in order to obtain some species abundances which were not finally included in the previous articles.

Subsequently, the species lists from these studies were completed with data taken from hand sampling by E. Montes de Oca and Q. Santiago leg., for Tonalaco (TON); F. J. Cabrero-Sañudo and N. Trotta-Moreu leg., for CUI; M. Dellacasa, I. Martínez, T. Pensado, Q. Santiago, and T. Suárez leg., for SJA; and J. Ari, M. Cruz, I. Martínez, P. Reyes, T. Suárez, and M. Zunino leg., for LDF; and from other published works by Dellacasa et al. 2002, for CUI and SJA; and by Arellano 2002, for SJA.

In order to describe the dung beetle communities of high mountain pastures situated in the Oriental Neovolcanic

Axis, some data from species were compiled.

Total richness of Aphodiinae, Scarabaeinae, and Geotrupinae species was obtained for each locality. For each species, known reproductive cycles were also consulted on literature (Cruz et al. 2002, Martínez 2005, Martínez and Suárez 2006). Geographic distribution of species was taken mainly from Delgado-Castillo and Márquez (2006), Dellacasa and Dellacasa (2005), Dellacasa and Stebnicka (2001), Dellacasa et al. (2002), Edmonds (1994), Galante et al. (2003), Howden (2003), Morón et al. (2003), Navarrete-Heredia and Deloya (2005), and Zunino and Halffter (1988). Biogeographic categories for each species were based on regions and dominions proposed by Morrone (2006).

RESULTS

Seven Scarabaeoidea species were found during the complete sampling period (February 2005 – February 2006), with a total of 1997 individuals. Samples encountered one Geotrupidae: Geotrupinae species, *Geotrupes* (*Halffterius*) *rufoclavatus* (Jekel, 1865); five Aphodiinae, *Blackburneus charmionus* (Bates, 1887), *Chilothorax ornatus* (Schmidt, A., 1911), *Gonaphodiellus opisthius* (Bates, 1887), *Oxyomus setosopunctatus* Schmidt A., 1911, and *Planolinellus vittatus* (Say, 1825); and one Scarabaeinae, *Onthophagus chevrolati* ssp. *chevrolati* Harold, 1869 (Table 1).

Species phenology and reproductive cycles.—Throughout all the sampling period in Tonalaco, the months of February, July, and November 2005, and February 2006 were those with highest species richness (4 to 6 species), whereas lowest richness (2 species) was seen in March and October 2005 and January 2006 (Table 1). For Aphodiinae, February, July, and November 2005 showed the highest richness (3 to 4 species), while the lowest richness (0 to

Table 1. Species gathered and individual abundances for the sampling near Tonalaco (Veracruz, Mexico) from February 2005 to February 2006.

	Dry Season				Rainy Season					Dry Season				
	II-7-2005	III-7-2005	IV-4-2005	V-2-2005	VI-6-2005	VII-13-2005	IX-2-2005	IX-26-2005	X-21-2005	XI-28-2005	XII-13-2005	I-24-2006	II-21-2006	TOTAL
Scarabaeidae: Aphodiinae														
Blackburneus charmionus (Bates, 1887)	8	-	-	-	-	-	-	-	-	2	-	-	2	12
Chilothorax ornatus (Schmidt, A., 1911)	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Gonaphodiellus opisthius (Bates, 1887)	-	-	5	10	861	411	20	54	123	47	21	-	-	1552
Oxyomus setosopunctatus Schmidt, A., 1911	1	-	-	-	-	5	-	-	-	-	-	-	-	6
Planolinellus vittatus (Say, 1825)	45	58	27	20	13	4	-	-	-	3	7	-	18	195
Scarabaeidae: Scarabaeinae														
Onthophagus chevrolati Harold, 1869	80	40	7	7	5	5	17	14	16	8	9	3	9	220
Geotrupidae: Geotrupinae														
Geotrupes (Halffterius) rufoclavatus Jekel, 1865	2	-	-	-	-	-	1	2	-	-	-	5	1	11

1 species) occurred in March, September, and October 2005, and January 2006. Geotrupinae richness was at a maximum in February, September, and January 2005 and February 2006, though with only one species each month and null during the rest of the year. For Scarabaeidae, a species richness of one was a constant throughout the whole year. No significant correlations were observed between species richness or species abundances and monthly mean, minimum, or maximum temperatures or precipitation, except for *G. opisthius*; nor were significant differences observed in species richness or abundances between rainy and dry seasons, except for *G. opisthius*.

The most abundant species was *G. opisthius* (Table 1). This species was active from April to December, presenting two population peaks, a higher one in June–July, and a smaller one in October. This species displayed a significant relationship to precipitation ($rs = 0.56$; $P = 0.047$) and there was a significant higher number of individuals captured on the rainy season ($t = -2.33$; df $= 11$; $P = 0.040$). Female individuals collected in May and June were maturing and ready for oviposition (Fig. 3). In July, all the females had laid eggs, and in August, 20% had. From August to December 2005, most (80% in August) or all the females were immature. With regard to males, in May, 60% were approaching a mature stage; the other 40% were fully mature males that had already copulated. From June to August, all the males found had copulated, as well as 10% of males in September. Immature males were observed from September (90% of males) to December.

Planolinellus vittatus showed a moderate number of individuals throughout the year (Table 1). This species was found from February to July and from November to December, showing its highest peak in February–March. This species seems to disappear when rains are at their highest point, though it has not been statistically confirmed. Maturing females and mature females before oviposition were found in March, June, July, and December 2005, and February 2006, whereas some females had already oviposited in March–July, November and December 2005, and February 2006 (Fig. 3). For males, the immature stage is present at least during two months, April (10%) and June (60%). Most of the remaining males were found maturing or mature before copulation in March to June, November, December 2005, and February 2006. Only a small proportion of males had already copulated, and these were observed in the months of March, May, December 2005, and February 2006.

The species *O. chevrolati* also presented a moderate number of individuals throughout the year (Table 1). *Onthophagus chevrolati* was active all year, presenting the two highest abundances in February–March and September–October. Its highest peak appeared to occur during the dry season, though statistically there are no abundance differences with the rainy season. All the mature females that had copulated were found from May to December, whereas most of the remaining females were maturing or mature without having oviposited (Fig. 3). Only a modest percentage of females in June (30%) were immature. All the males observed throughout the year were maturing or already mature, before or after copulation, and no immature individual at all appeared. Mature males that had not copulated were found in the months of April and June, and from August to February. Males that had copulated were the majority of individuals in March, July, January, and February, but a small percentage was observed in June and August.

Blackburneus charmionus and *C. ornatus* were active during the dry season,

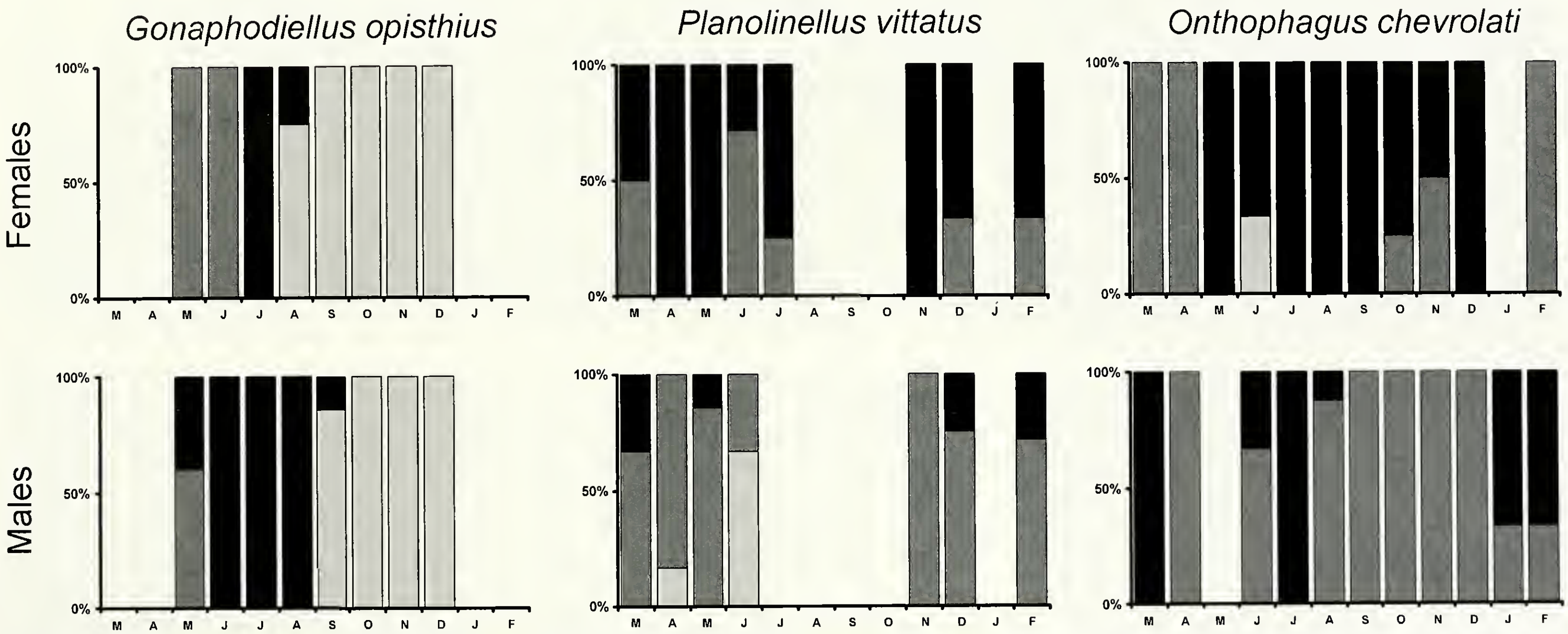

Fig. 3. Monthly percentages of reproductive stages for the three most abundant species gathered near Tonalaco, Veracruz, Mexico, from March 2005 to February 2006. For females, light grey portions of the bar represent the immature stage, dark grey portions the stage before oviposition, and black portions the stage after oviposition. For males, light grey bar portions represent the immature stage, dark grey portions the stage before copulation, and black portions the stage after copulation.

whereas *O. setosopunctatus* and *G.* (*H.*) *rufoclavatus* appeared in both seasons. Nevertheless, the first three species only showed sporadically in low numbers of individuals and in no more than three scattered months, so they were not considered for examination of their reproductive cycles. Data for *G.* (*H.*) *rufoclavatus* have been not included in this study — those data will be integrated in a future article along with data about its distribution (Trotta-Moreu et al., in press).

Completeness of inventories and characterization of dung beetle communities.—Predicted species richness values for ACE were 6 (LDF), 7 (CUI), and 8 (SJA and TON), so the sampling most likely recovered between 87.5% and 100% of total dung beetle species present at the localities. According to Chao2, predicted species richness values were 6 (LDF) and 7 (CUI, SJA, and TON), so 100% of present dung beetle species had been recovered during the samplings. It must be considered that estimators are just notifying that the samplings have a suitable invested effort, since some other species had been cited for these localities at some point.

Table 2 summarizes the species observed in each of the four high mountain localities. Of a total of 21 observed species, three are observed in all four communities: two Aphodiinae, *O. setosopunctatus*, and *P. vittatus*, and one Scarabainae, *O. chevrolati* (although three of the localities have the nominal *chevrolati* subspecies and the LDF locality has the subspecies *retusus* Harold, 1869). Two Aphodiinae species have been also captured in three of these communities: *C. hogei* and *G. opisthius*. A total of twelve species have been cited from only one of these communities.

The greatest total species richness has been observed at CUI (11 species), whereas SJA shows 10 species, LDF 9 species, and TON 8 species. The observed species richness for Aphodiinae is similar in all the localities (6–8 species). CUI is the only locality where three Scarabaeinae species have been cited; the rest only have one. For Geotrupinae, there is only a different species in each locality.

Reproductive cycles for each species taken from literature have been also added to Table 2. A great number of reproductive cycles remain yet to be analyzed. Most of the studied Aphodiinae species behave as univoltine. Only one reproductive cycle for Scarabaeinae species is known, and it is multivoltine. For Geotrupinae, no reproductive cycle of cited species has been previously examined.

Table 2 also shows the geographic distribution of species. Most of the species are restricted to Mexican Transition Zone (MTZ) and Mesoamerican distributions. Aphodiinae species show basically distributions spread on both regions. However, three species of Aphodiinae are exclusively endemic to the MTZ, and other three have a wide distribution. For Scarabaeinae two species are restricted to the MTZ, whereas another species is distributed on both the MTZ and the Mesoamerican dominion. All observed Geotrupinae species are endemic to the MTZ.

Discussion

Phenology and reproductive cycles.—In the present study, all dung beetle species showed periods of presence and absence throughout the year, except for *O. chevrolati*, which is found all year.

Gonaphodiellus opisthius is a markedly univoltine species, associated with precipitations and the rainy season (Cruz et al. 2002). The two population peaks observed throughout the year represented different generations (Cruz et al. 2002): one from May to August, corresponding to individuals born the previous year, which mature, reproduce,

Table 2. Matrix of species abundances for each dung beetle community studied on high mountain pastures, including known reproductive cycles and geographic distributions. (CUI, Cuiyachapa; LDF, Llano de las Flores; SJA, San José Aguazuelas; TON, Tonalaco). Number of months of continued samplings between parenthesis. Data sources (completed with data from their record sheets): CUI, Cruz et al. 2002; SJA, Martínez 2005; LDF, Martínez and Suárez 2006; TON, present study. * Additional data (only presences): CUI, Dellacasa et al. 2002, and samplings by hand [F. J. Cabrero-Sañudo and N. Trotta-Moreu leg.]; SJA, Arellano 2002, Dellacasa et al. 2002, and samplings by hand [M. Dellacasa, I. Martínez, T. Pensado, Q. Santiago, and T. Suárez leg.]; LDF, samplings by hand [J. Ari, M. Cruz, I. Martínez, P. Reyes, T. Suárez, and M. Zunino leg.]; TON, samplings by hand [E. Montes de Oca and Q. Santiago leg.]). Unknown reproductive cycles have been marked with a question mark. Information for species geographic distributions has been taken from Delgado-Castillo and Márquez (2006), Dellacasa and Dellacasa (2005), Dellacasa and Stebnicka (2001), Dellacasa et al. (2002), Edmonds (1994), Galante et al. (2003), Howden (2003), Morón et al. (2003), Navarrete-Heredia and Deloya (2005), and Zunino and Halffter (1988), and distributions categories were based on Morrone (2006), except for wide distributed species.

	CUI (13)	LDF (12)	SJA (12)	TON (13)	Reproductive Cycle	Geographic Distribution
Scarabaeidae: Aphodiinae						
Agrilinus azteca (Harold, 1863)	*	-	-	-	?	MTZ, Mesoamerican
Blackburneus charmionus (Bates, 1887)	*	-	-	12	?	MTZ, Mesoamerican
Blackburneus guatemalensis (Bates, 1887)	-	*	*	-	?	MTZ, Mesoamerican
Blackburneus sp. *aff. diminutus* (Bates, 1887)	-	-	-		?	MTZ, Mesoamerican
Cephalocyclus durangoensis (Bates, 1887)	-	379	-	-	Univoltine	MTZ
Cephalocyclus hogei (Bates, 1887)	6964	*	228	-	Univoltine	MTZ, Mesoamerican
Chilothorax ornatus (Schmidt, A., 1911)	-	-	108	1	Univoltine	MTZ
Gonaphodiellus opisthius (Bates, 1887)	19155	436	-	1552	Univoltine	MTZ, Mesoamerican
Labarrus pseudolividus (Balthasar, 1941)	*	-	-	-	?	Afrotropical, Australian, Nearctic, Neotropical, Oriental
Liothorax innexus (Say, 1835)	-	-	*	-	?	Californian, Continental Nearctic, MTZ, Mesoamerican, Antillean
Liothorax levatus (Schmidt, A., 1907)	-	164	116	-	Univoltine	MTZ, Mesoamerican
Oxyonus setosopunctatus Schmidt, A., 1911	*	*	37	6	?	MTZ, Mesoamerican
Planolinellus vittatus (Say, 1825)	211	1238	*	195	Multivoltine	Holarctic
Trichonotuloides glyptus (Bates, 1887)	-	-	9	-	?	MTZ
Scarabaeidae: Scarabaeinae						
Onthophagus aureofuscus Bates, 1887	1	-	-	-	?	MTZ
Onthophagus chevrolati chevrolati Harold, 1869	300	-	71	220		
retusus Harold, 1869	-	312	-	-	Multivoltine	MTZ
Phanaeus amethystinus amethystinus Harold, 1863	2	-	-	-	?	MTZ, Mesoamerican

Table 2. Continued.

	CUI (13)	LDF (12)	SJA (12)	TON (13)	Reproductive Cycle	Geographic Distribution
Geotrupidae: Geotrupinae						
Geotrupes (Halffterius) rufoclavatus Jekel, 1865	-	-	-	11	?	MTZ
Geotrupes (Onthotrupes) herbeus Jekel, 1865	-	-	1	-	?	MTZ
Geotrupes (Onthotrupes) sobrinus Jekel, 1865	30	-	-	-	?	MTZ
Geotrupes (Onthotrupes) viridiobscurus Jekel, 1865	-	45	-	-	?	MTZ

and finally die; and another from September to December, corresponding to the new generation, composed of immature imagoes.

In contrast to *G. opisthius*, the phenologies of *P. vittatus* and *O. chevrolati* are possibly associated with the dry season, with higher numbers of individuals when rains are lower (as at Llano de las Flores, Oaxaca; Martínez and Suárez 2006). Mature *P. vittatus* imagoes probably take refuge during the most humid and driest conditions, and when the time is suitable for them they come up and reproduce. Once they copulate, males disappear, whereas females outlast the males briefly, during which time they lay eggs. This phenology is also similar to that observed at Las Vigas de Ramírez, Veracruz, and under laboratory conditions, where they apparently reproduce all year (I. Martínez M., unpublished observations).

Onthophagus chevrolati females lay eggs during the rainy season, whereas in the driest months, they remain mature but do not lay eggs. Males quickly mature and probably die after copulation during the rainy season, although many males survive the driest months of the year and the beginning of the rainy season after having copulated. It is possible that, just like *P. vittatus*, these individuals also mate whenever conditions are favourable.

Dung beetle communities from the Oriental Neovolcanic Axis.—This study is the fourth of this sort carried out in a high mountain dung beetle community on the Oriental Neovolcanic Axis. The San José Aguazuelas study by Martínez (2005) was conducted at roughly 6.6 km distant in a straight line from the Tonalaco study site. The Cuiyachapa study was situated around 50 km away, in a straight line to the south of these two previous localities (Cruz et al. 2002). Finally, Llano de las Flores sampling was carried out around 230 km in a straight line to the southeast of those localities (Martínez and Suárez 2006). Despite distances, the four localities share some characteristics as regards to their dung beetle communities.

First of all, the four localities hold similar dung beetle species richness values for the three subfamilies considered, independently and jointly. Only Cuiyachapa locality apparently presents a greater number of Scarabaeinae species, although two of these species are possibly random vagrants with low numbers of individuals (*O. aureofuscus* and *P. amethystinus*).

Six species are the most abundant taxa and are present in at least two of these high mountain pastures localities (*C. hogei, C. ornatus, G. opisthius, L. levatus, P. vittatus*, and *O. chevrolati*; Table 2). *Cephalocyclus durangoensis* showed also a high number of individuals at Llano de las Flores location, and *O. setosopunctatus* was also captured at one time in all localities. Thus, basically, these eight species could portray the dung beetles communities composition at the Oriental Neovolcanic Axis localities.

Phenology and reproductive cycles of most of these species have been previously studied (Cruz et al. 2002, Martínez 2005, Martínez and Suárez 2006). In general terms, most Mexican high mountain dung beetle species would show marked seasonal activity patterns in the field, and would be probably univoltine. Reproductive cycles of the four Geotrupinae species cited for the surveyed localities are unknown, although possibly they are also univoltine, as it has been suggested for *G. rufoclavatus* (Trotta et al., in press) and observed for another high mountain species from the Sierra Madre Occidental, *Geotrupes (Megatrupes) cavicollis* Bates, 1887 (Halffter et al. 1980, 1985).

Dung beetles tend to adjust their activity and reproductive periods to optimum climatic and environmental conditions, as other insects (Engelmann 1970, Raabe 1986). Thus, most species at high mountain pastures would present short reproductive cycles corresponding to suitable seasons. This behaviour has been also observed on other dung beetle species, especially from the Western Palaearctic (Kirk and Wallace 1990, Martínez 2001). Nevertheless, as it has been examined in the present study, *P. vittatus* and *O. chevrolati* are an exception, being active during all the year whenever weather conditions are appropriate, and producing several generations per year.

Two principal dung beetle activity periods may be observed through the year: one at the beginning of the rainy season (basically from the end of May to the beginning of August) and another from the end of the rainy season to the middle of the dry season (from August to February). The first period is characterized by species as *C. durangoensis, C. hogei* and *G. opisthius*. These species would need the first rains and the rise of temperatures at high mountain localities in order to breed (Cruz et al. 2002, Martínez 2005, Martínez and Suárez 2006). Species as *L. levatus, C. ornatus* and, possibly, *O. setosopunctatus* stand out at the second period. These species would probably appear when there are still some regular rains, the temperature is moderate, and the soil is still moist (Martínez 2005, Martínez and Suárez 2006). *Planolinellus vittatus* and *O. chevrolati* are present through all the year, although they show a greater affinity to the dry season.

As regards to geographical distribution, most Oriental Neovolcanic Axis Aphodiinae display greater ranges than Scarabaeinae or Geotrupinae. Most high mountain Aphodiinae extend their distribution to the MTZ and Mesoamerica, whereas most Scarabaeinae and Geotrupinae are only present at the MTZ (Geotrupinae species show some regionalization, so their ranges could be even more limited, as shown on Table 2). Most of the dung beetles present at the Oriental Neovolcanic Axis would be Nearctic elements *sensu* Halffter (1987, 2006), that is, taxa with a predominantly northern affinity, of recent penetration and development, and restricted to orographic systems of the MTZ and Centro America. Some exceptions to this are, for example, *P. vittatus* (as a matter of fact, one species which has been also observed as multivoltine), with a Holarctic distribution and possibly a Paleo-American element *sensu* Halffter (1987, 2006) – early immigrated taxa from northern latitudes –; *G. opisthius* and *Blackburneus* species, with southern affinities and possibly Montane Meso-American elements *sensu* Halffter (1987, 2006) – taxa with an early South American origin and linked to mountains –; and, *L. pseudolividus*, also with southern affinities and probably a Neotropical element *sensu* Halffter (1987, 2006) – a species with a relatively recent arrival from South America and related to tropical lowlands –, which has been able to reach higher elevations.

The Tonalaco dung beetle community is the poorest, although only slightly, in species richness compared to the other three localities where similar sampling techniques were applied. According to several analytical studies about land evolution during the 20th century in Xico territory, the municipality encompassing Tonalaco and its surrounding areas, this land has suffered a great environmental degradation in recent years (Hoffmann 1992, 1993). Thus, this mountain has been characterized by a loss of habitats (mainly changes in traditional land uses and crops, forestry and illegal deforestation, and fragmentation of larger to smaller-scale farming; Hoffmann 1992, 1993) and uncontrolled chemical applications (mainly herbicide applications to reduce weeds from pastures and aggressive techniques to remove parasites from livestock, survey to cattle-raisers from Xico municipality, Martínez et al. unpublished data).

As many mountain dung beetle species of the Mexican Transition Zone are usually widespread, it is probably that most of them are not directly threatened by complete extinction. But these habitat changes at Tonalaco are only a sample of progressively generalized agricultural tendencies for the productive lands of the Oriental Neovolcanic Axis and other mountain ranges from the Mexican Transition Zone (Hoffmann 1992), that might decimate these mountain species locally and widely in the near future. Considering that, it is important to keep in mind the irreplaceable loss of biodiversity that habitat degradation could hasten, beyond the loss of the ecological and parasite-controlling role that dung beetle species play in local pasture systems.

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